Changes in Leaf Osmotic and Elastic Properties and Canopy Structure of Strawberries under Mild Water Stress

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Abstract. Field-grown strawberry (*Fragaria × annanasa* Duch. cv. Chandler) plants were subjected to two irrigation regimes from Nov. 1989 to July 1990 to evaluate the physiological and morphological effects of mild water stress. Irrigation was applied when soil matric potential reached -10 and -70 kPa for the wet and dry treatments, respectively. During the spring, these regimes did not promote significant changes in plant water relations, transpiration rates, plant morphology, or canopy architecture. However, during the summer, after several stress cycles, significant differences between treatments were observed. Pressure-volume curves of dry-treatment plants indicated that leaf osmotic potentials, measured at full and zero turgor, decreased 0.2 to 0.4 MPa. This decrease in osmotic potential also was accompanied by a 50% increase in the modulus of elasticity for these water-stressed plants compared to well-watered plants. Dry-treatment plants also showed stress avoidance mechanisms in changes of whole-plant morphology and canopy architecture, from monolayer to polylayer leaf distribution and leaf orientation from south to north. Despite what would appear to be useful drought-resistance strategies, there was significantly lower fruit production by plants grown under the dry treatment.

Horticultural crops and their wild ancestors have developed many mechanisms to survive water stress, including escape, tolerance, and avoidance of tissue water deficits. Avoidance of water stress includes changes in leaf area, anatomy, orientation, and color, among others (Jones, 1980). Tolerance to water stress usually involves two mechanisms, osmotic adjustment and changes in elastic properties of tissues (Morgan, 1984; Munns, 1988; Roberts et al., 1981; Robichaux et al., 1986; Turner, 1986).

In our part of the Mediterranean region, strawberry crops often develop moderate water stress as a consequence of either inappropriate or untimely irrigation scheduling, which often results in decreased yields (Marfà et al., 1990; Serrano et al., 1992). A better understanding of plant adaptation to drought stress may help to enhance irrigation management practices. Our objectives were to evaluate the physiological changes promoted by moderate water deficits in field-grown strawberry plants

and to assess the contribution of putative adaptation mechanisms to turgor maintenance.

'Chandler' strawberry plants were planted at our center in El Maresme, Catalonia (lat. 41°25'N, long. 2°23'E), on 10 Nov. 1989 and grown until 11 July 1990 in a Typic Xerorthent soil under a tunnel covered with thermic polyethylene plastic film. During the 2 months after planting, irrigation was applied when soil matric potentials reached -20 kPa. Thereafter, two irrigation treatments were established in two plots of four replication beds. Each plot was 6 x 4.5 m, with plants set every 30 cm within the rows. Rows were 32 cm apart. Plant density was 6.4 plants/m².

Irrigation was applied in each plot when soil matric potential reached -10 kPa (wet) and -70 kPa (dry). Soil matric potentials were determined as the average from six tensiometers (Soilmoisture 2725; Soilmoisture, Santa Barbara, Calif.) located 10 and 20 cm deep and 15 cm apart from the emitter in each plot. Water was supplied by trickle irrigation using turbulent-flow emitters spaced 30 cm apart, with a flow rate of 2 liters·h⁻¹.

At each irrigation, a nutrient solution was applied. Tap water was adjusted according to Steiner's method (Steiner, 1966) to obtain the nutrient equilibria of 1:0.5:1.8 and 1:0.7:2.5 (N-P₂O₅-K₂O) for vegetative and reproductive periods, respectively. Because different irrigation regimes can alter the nutritional status of treated plants and bias results, we analyzed the N content of leaf and fruit samples. No significant differences were found ($P = 0.05$) in fruit and leaf N content between the two irrigation treatments. Mean leaf N content was 1.98 ± 0.14 SE and 2.13 ± 0.24 SE, and fruit N content was 1.31 ± 0.16 SE and 1.29 ± 0.05

SE, for -10 kPa and -70 kPa treatments, respectively.

Mature leaves from the wet and dry plots were randomly selected during the mornings of 24 Apr. and 11 July 1990. They were excised, immediately sealed in plastic bags containing some water, and transported to the adjacent laboratory. Petioles were recut under water, set in beakers filled with water, and the beaker with leaf was then enclosed in a plastic bag to rehydrate for 48 h at 5°C in darkness. Five water-saturated leaves were measured for each irrigation regime. They were weighed and then allowed to dehydrate by transpiration for a period during which they were repeatedly inserted in a pressure chamber (Soilmoisture 3005) to determine xylem water potential (Ψ_x) (Kikuta and Richter, 1986). Data for initial saturated weight, intermediate fresh weight corresponding to values for Ψ_x , and final dry weight were used to calculate the relative water content (RWC). The RWC and the corresponding Ψ_x were plotted as a "Type II" ($\Psi_x^{-1} \times \text{RWC}$) transformation (Tyree and Richter, 1981, 1982). The parameters derived from pressure-volume (P-V) curves were osmotic potential at full ($\Psi_{\pi 100}$) and at zero turgor ($\Psi_{\pi 0}$), and leaf volumetric elastic modulus (ϵ) (Sobrado, 1986; Turner, 1988). At the same time, cuticular water loss rates were obtained gravimetrically on the same leaves used for P-V curve measurements (Savé, 1986; Sveningsson and Liljenberg, 1986). We considered cuticular water loss rates to be the values obtained below the point of zero turgor. Specific leaf weight (SLW) also was calculated using these same leaves.

At the end of the experiment, in July, we described canopy architecture for plants in the two irrigation regimes. Leaf area index (LAI) was calculated by measuring the central leaflet length of 12 plants from each treatment. Total area was then estimated as $\text{area (cm}^2\text{)} = 21.49 \times \text{length (cm)} - 52.62$ ($n = 16$ and $r^2 = 0.9360^{***}$), which was established experimentally. We classified leaves as south-, north-, and zenith-oriented. We also counted the leaves positioned every 5 cm from the top to the bottom of the canopy. At the same time, root biomass was determined by digging ten 35-cm-diameter and 25-cm-deep cores, each containing a plant, from each irrigation treatment. Cores were washed free of soil, and the roots were weighed. Fruit were harvested at 3-day intervals, from 110 to 248 days after planting.

No significant differences were found in the parameters between irrigation treatments in the spring (Table 1). This may have been due to the low evaporative demand of the atmosphere and also to too few accumulated stress cycles. In April, 16 stress cycles had accumulated in the wet plots, while only three stress cycles had occurred in the dry plots. Average solar radiation was $17.5 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$, and calculated evapotranspiration (ETP) Penmann was 100 mm. In contrast, the daily average solar radiation in July was $23.9 \text{ MJ}\cdot\text{m}^{-2}$, and the calculated ETP Penmann was 151 mm. By that time, the dry and wet plots had accumulated 16 and 39 stress cycles, re-

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Table 1. Seasonal patterns of ecophysiological parameters of strawberry plants subjected to two irrigation levels.^z

Measurement ^y	Spring		Summer	
	Wet ^x	Dry	Wet	Dry
Hydric				
$\Psi_{\pi 100}$ (MPa)	-1.59 ± 0.06^{ns}	-1.70 ± 0.09^{ns}	$-1.43 \pm 0.05^*$	$-1.85 \pm 0.08^*$
$\Psi_{\pi 0}$ (MPa)	-1.98 ± 0.05^{ns}	-1.99 ± 0.09^{ns}	$-1.89 \pm 0.03^*$	$-2.10 \pm 0.04^*$
ϵ (MPa)	6.17 ± 0.20^{ns}	6.96 ± 0.18^{ns}	$5.46 \pm 0.66^*$	$8.18 \pm 0.36^*$
TR _c ($\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{s}^{-1}$)	1.13 ± 0.06^{ns}	1.06 ± 0.07^{ns}	1.04 ± 0.28^{ns}	1.23 ± 0.10^{ns}
Morphological and productivity				
SLW ($\text{mg}\cdot\text{cm}^{-2}$)	6.37 ± 0.11^{ns}	6.35 ± 0.09^{ns}	$5.86 \pm 0.19^*$	$7.83 \pm 0.08^*$
LAI	2.61 ± 0.12^{ns}	1.98 ± 0.10^{ns}	$5.10 \pm 0.27^*$	$2.55 \pm 0.14^*$
Accumulated fruit production ($\text{kg}\cdot\text{m}^{-2}$)	$1.84 \pm 0.16^*$	$1.41 \pm 0.14^*$	$7.81 \pm 0.43^*$	$4.98 \pm 0.49^*$

^xWet is -10 kPa and dry is -70 kPa of soil matric potential.

^y $\Psi_{\pi 100}$ and $\Psi_{\pi 0}$ are osmotic potentials at full and zero turgor, respectively, and ϵ is the volumetric modulus of elasticity. TR_c is cuticular transpiration rate, SLW is specific leaf weight, and LAI is leaf area index.

^zEach value is the mean of five observations $\pm$ SE.

^{ns}, *Nonsignificant or significant, respectively, between treatments at $P \leq 0.05$ by analysis of variance.

spectively. In July, there were significant differences in osmotic potential at full and zero turgor, volumetric elastic modulus, SLW, LAI, leaf distribution, and orientation or fruit yield between treatments (Table 1). The $\Psi_{\pi 100}$ and $\Psi_{\pi 0}$ were 29% and 11% lower, respectively, in the dry treatment, suggesting some degree of osmotic adjustment in response to water deficits (Morgan, 1984; Turner, 1986; Turner and Jones, 1980). This decrease in the dry treatment can be caused partially by the concentration of solutes (Ackerson and Hebert, 1981; Sobrado, 1986) due to a small reduction in cell size as shown by the increase in SLW. The high values of ϵ in the dry treatment (ϵ was 50% higher in stressed than in well-watered plants, and it was 16% higher in summer than in spring) indicate lower tissue elasticity. This decrease in tissue elasticity causes an increase in the magnitude of the change in turgor pressure for a given fractional change in tissue water content (Myers and Neales, 1986; Robichaux et al., 1986). There were no significant differences in cuticular transpiration rates (TR_c) between irrigation treatments (Table 1).

There were also changes in LAI, leaf angle, and leaf anatomy. Dry-treatment plants had a 50% lower LAI than wet-treatment plants (Table 1). This change in LAI provides an important alternative for water loss regulation (Jones, 1980). We also found differences in canopy architecture between irrigation regimes. Plants from the dry treatment tended to form a polylayer canopy, with leaves distributed along a vertical profile, while plants from the wet treatment tended to form a monolayer canopy, as shown by the vertical profile of leaf distribution (Table 2). North and south leaf orientation was also clearly distinct in the irrigation treatments (Table 2). Most leaves of plants in the wet treatment were south-oriented, while most leaves of plants in the dry treatment were north-oriented. Both modifications in canopy architecture suggest a strategy to increase light absorption efficiency while controlling water loss (Fisher, 1986; Givnish, 1986; Morris, 1989; Nobel, 1983).

Root biomass was similar for the irrigation regimes. In July, the root biomass was 4.60 ± 0.91 for wet and 4.23 ± 0.83 g dry weight/plant

for dry treatments. The lack of differences may be explained by the irrigation system employed in which only a fraction of the available soil volume was wetted (Renquist et al., 1982).

From our results, we can conclude that strawberry plants in the wet treatment were subjected to very mild water stress and showed a tolerance mechanism based on high elasticity of tissues, thus permitting a greater use of nutrients and assimilates for growth (Munns, 1988), while turgor-mediated processes, such as elongate growth and photosynthesis, could be maintained (Bradford and Hsiao, 1982). Strawberry plants in the dry plots maintained leaf turgor pressure by tolerance and avoidance mechanisms (Levitt, 1980; Morgan, 1984). These plants tolerated drought by actively accumulating solutes that allowed osmotic adjustment. Together with less elastic tissues, this mechanism allows leaves to reach more negative water potentials for a given change in water volume, facilitating continued water uptake from drying soil (Bowman and Roberts, 1985). Moreover, dry-treatment plants developed mechanisms of drought avoidance. They had higher SLW, their LAI was lower, and leaves were mostly oriented to

Table 2. Distribution and orientation of strawberry leaves at the end of the production period in the summer for plants subjected to two irrigation regimes.

Characteristic	Wet ^x	Dry
Leaf canopy (%)		
Vertical distribution (cm above soil)		
>25 to 30	37 ± 6^y	7 ± 4
>20 to 25	26 ± 5	23 ± 8
>15 to 20	13 ± 4	23 ± 5
>10 to 15	15 ± 2	25 ± 5
>5 to 10	8 ± 1	15 ± 2
0 to 5	1 ± 0.6	7 ± 2
Orientation		
North	17 ± 2	41 ± 6
Zenith	31 ± 2	38 ± 8
South	52 ± 4	21 ± 2

^xWet is -10 kPa and dry is -70 kPa of soil matric potential.

^yEach value is the mean of 10 observations $\pm$ SE.

the north. They also were distributed randomly in height instead of mainly in the upper part of the canopy as in the wet treatment (Givnish, 1986; Jones, 1980). In spite of these adaptations, final fruit production in the dry treatment was lower than in the wet treatment (Table 2).

Thus, 'Chandler' plants developed several physiological adaptations to water stress, such as osmotic adjustment, similar to that described by Archbold and Zang (1991) in *Fragaria virginiana* Duch. and *F. chiloensis* (L.) Duch. However, in contrast with the results obtained by those authors, we also found morphological adaptations that seemed to play an important role in the adaptation of this strawberry cultivar to drought stress.

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